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Prey size affects the costs and benefits of group predation in nymphs of the predatory stink bug *Andrallus spinidens* (Heteroptera: Pentatomidae)

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Abstract Group predation promotes foraging efficiency because it increases the size of prey that can be killed and improves hunting success compared to solitary predation. However, group predation may increase competition among group members during feeding. Earlier studies have focused on the advantages of group predation, but little is known about the costs and benefits of group predation for individual members of the group. Here, we show that the costs and benefits of group predation for individuals of the predatory stink bug *Andrallus spinidens* vary with prey size in laboratory experiments. We found that when *A. spinidens* fed on small prey, group predation did not significantly increase foraging efficiency but did increase competition for food among group members. In contrast, when prey was large, group predation promoted foraging efficiency, and competition over food was not detected. Our results suggest that group predation by *A. spinidens* nymphs is advantageous for individual members because it enables each member to hunt larger prey that could not be hunted alone. However, when group size was large or prey size was small, group predation increased competition among group members.

Keywords Group predation · Group size · Prey size · Asopinae · *Andrallus spinidens*

Introduction

Group predation occurs in a wide range of taxa, including insects (e.g., Chadab and Rettenmeyer 1975; Dejean et al. 2013), social spiders (e.g., Burgess 1976; Kim et al. 2005), fish (e.g., Bshary 2006), birds (e.g., Bednarz 1988), and mammals (e.g., Creel and Creel 1995). In particular, social carnivores have been the focus of much research on group hunting behavior (reviewed by Bailey et al. 2013; Krause and Ruxton 2002). Group predation is infrequent in insects, but has been reported in eusocial insects (Breed et al. 1987; Schatz et al. 1997; Daly-Schveitzer et al. 2007), first instar larvae of aphidophagous ladybird beetles (Hemptinne et al. 2000; Moore et al. 2012), some assassin bug nymphs (Inoue 1985; Dejean et al. 2013), and nymphs and adults of some predaceous pentatomids (Manley 1982; Matlock 2005). Group predation promotes foraging efficiency because it allows the capture of larger prey and can improve hunting success compared to solitary predation (Inoue 1985; Bednarz 1988; Creel and Creel 1995). However, if group size is large or prey size is small, group predation may increase competition among group members during feeding (Krause and Ruxton 2002). Thus, the costs and benefits of group predation should depend on the combination of group size and prey size.

While many studies have examined the costs and benefits of group predation, less attention has been paid to the costs and benefits for individuals in the group. To clarify individual costs and benefits, examining predation behavior with different group sizes and prey sizes is important. This is difficult with vertebrate predators because of their long

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life span, complex social ecology, and low population density. Therefore, we investigated the costs and benefits of group predation at the individual level with nymphs of a predatory stink bug.

The predatory stink bug *Andrallus spinidens* is widely distributed in tropical and warm-temperate zones worldwide. This bug inhabits grasslands, paddy fields, and vegetable fields and kills many types of lepidopteran, coleopteran, and hymenopteran larvae (Tomokuni et al. 1993). In fields, several *A. spinidens* nymphs are commonly found feeding on a single prey (Manley 1982; Fig. 1). The gregarious behavior is most strongly expressed in the first two instars and to a lesser degree in the third instar. Fourth and fifth instars are mostly solitary (Manley 1982). *A. spinidens* uses extraoral digestion and attacks by inserting stylets into the prey body (Cohen 1998; Zibae et al. 2012). This attack behavior is easy to observe, making the nymphs of *A. spinidens* well suited for tests on the individual effects of group predation.

In this study, we examined the costs and benefits of group predation at the individual level in *A. spinidens* nymphs. Capture success of juvenile predators generally declines as prey size/predator size ratio increases (Nakazawa et al. 2013), and handling time increases as prey size increases (Dixon 1959). To study the effect of group predation on the prey size, we marked nymphs for individual identification and conducted behavioral observations. We counted the number of attacks by each nymph, recorded hunting time, and estimated predation success and weight gain. We compared these data between different group sizes and prey sizes.

Materials and methods

Study species

Adults and nymphs of the predatory stink bug *A. spinidens* were collected from sweet potato fields in Takanabe, Miyazaki Prefecture, Japan on 10–11 September 2007 and 2–5 September 2008. *A. spinidens* nymphs were usually found in groups of 2–80 individuals (Hyodo, unpublished data). Each group was reared in jars (top: 120 mm diameter; bottom: 100 mm diameter; 55 mm height) containing wet cotton to maintain humidity. The entrances of jars were covered with nylon mesh. The jars were kept under 16-h light and 8-h dark photoperiod conditions (light period, 0700–2300 hours) at 25 ± 2 °C. Fourth to sixth instar larvae of *Spodoptera litura* were used as prey. We provided distilled water and one prey per nymph every 2–3 days. We collected newly molted adults and placed two to three males and two to three females in jars that were kept under the same conditions as the nymphs. The deposited eggs

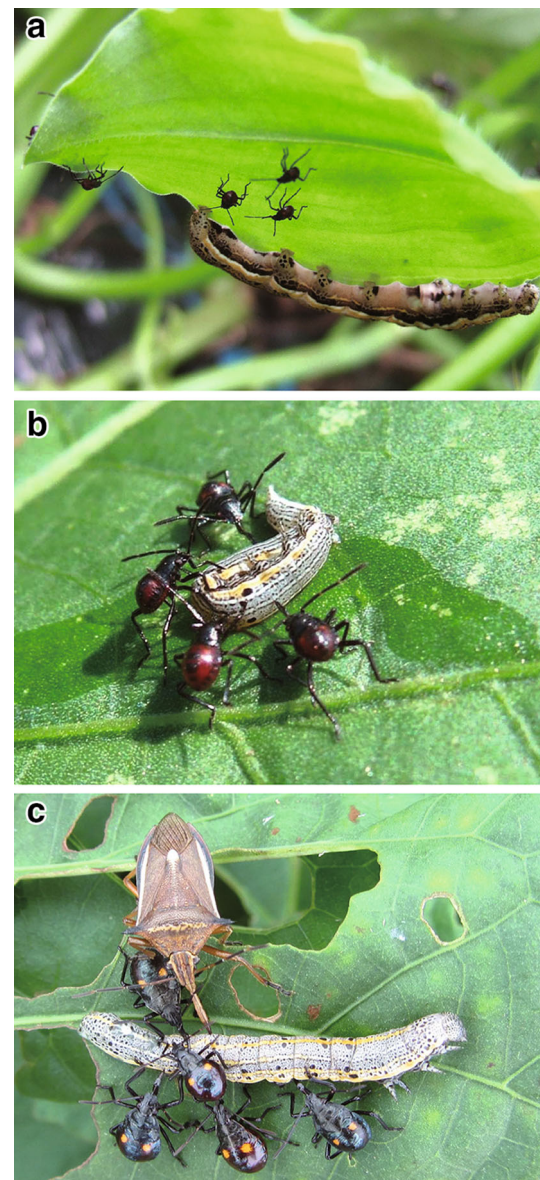


Fig. 1 Group predation by the stink bug *Andrallus spinidens*. **a** A group of second instar nymphs of *A. spinidens* pursuing a caterpillar of *Aedia leucomelas*. **b** Group feeding by second instar nymphs of *A. spinidens*. **c** A group of third and fourth instar nymphs of *A. spinidens* feeding on a caterpillar with an adult

were transferred to Petri dishes (90 mm diameter, 20 mm height) with cotton moistened with distilled water. First instar nymphs only suck water until they molt into the second instar (Manley 1982). In all experiments, we used F₁ and F₂ instar nymphs within 24 h of molting.

We used *S. litura* as prey in all experiments because they were observed being preyed upon by *A. spinidens* in the field (Shintani et al. 2010). *S. litura* was reared on an artificial diet (Insecta-LFS; Nihon Nosan Kogyo, Yokohama, Japan) at 25 ± 2 °C under a 16-h/8-h (light/dark) cycle. In the experiments, we used third, fourth, and sixth

instar larvae of *S. litura* as prey, which had mean weights of 15.1 ± 0.7 mg (SE, $n = 41$), 34.4 ± 1.6 mg ($n = 33$), and 674.7 ± 20.1 mg ($n = 21$), respectively.

Experiment

To examine the costs and benefits of group predation for individual *A. spinidens* nymphs, we recorded the number of attacks, hunting time, estimated predation success, and weight gain for each individual. Then, we compared these values among different group sizes. *A. spinidens* nymphs were individually marked with a paint marker (paint marker PC-1 M; Mitsubishi, Tokyo, Japan) and weighed using an electronic balance (JPN-189 W; Chyo Balance, Kyoto, Japan). One, two, or four nymphs were placed in Petri dishes (90 mm diameter, 20 mm height) having cotton moistened with distilled water. In tests of two and four individuals, the nymphs used were from the same egg mass. We then added one larva of third, fourth, or sixth instar *S. litura* to the center of the Petri dish. We prepared 16 replications for single nymph faced with third and fourth instar *S. litura* and two nymphs faced with fourth instar *S. litura*; 20 replications for two nymphs faced with third instar *S. litura*; 15 replications for four nymphs faced with third and fourth instar *S. litura*; 19 replications for single and two nymphs faced with sixth instar *S. litura*; and 17 replications for four nymphs faced with sixth instar *S. litura*. We recorded individual's attack behaviors for 2 h with uninterrupted direct observation or a digital video camera (NV-GS320; Panasonic, Tokyo, Japan). We recorded the following predator behaviors: (1) touch: light contact on the prey with its antennae or other parts of its body; (2) attack: insertion of stylets into the prey body; (3) prey paralysis: immobilization of the prey after insertion of its stylets; and (4) retreats: the predator retreats after defensive movements of the prey (Lemos et al. 2005). We recorded the number of successful attacks as the number that led to prey paralysis. We defined hunting time as the time from “touch” to “prey paralysis”. If the predators failed to eat within 2 h, the test was terminated. After the predators stopped feeding, they were weighed, and weight gain was calculated as the final weight minus initial weight. All experiments were started between 1300 and 1900 hours.

Statistical analysis

We used a two-way ANOVA to analyze the number of attacks and hunting time using prey instar and predator group size as factors for categorical data. We used Tukey's honest significant difference (HSD) post hoc test when the ANOVA showed a significant P value ($P < 0.05$). We used Fisher's exact probability test to analyze the predation

success of *A. spinidens* nymphs on *S. litura* larvae. We compared the weight gain of *A. spinidens* nymphs using a Kruskal–Wallis test with sequential Bonferroni correction. All analyses were performed using JMP v.5.1.2 (SAS Institute).

Results

Number of attacks per nymph

Both the group size of *A. spinidens* and the prey instar significantly influenced the number of attacks by each nymph ($P < 0.001$, two-way ANOVA; Table 1). *A. spinidens* nymphs made significantly more attacks when hunting upon sixth instar larvae of *S. litura* than hunting upon third and fourth instar larvae ($P < 0.05$, Tukey's HSD). In the test of sixth instar larvae, groups of four predators made significantly more attacks per individual nymphs than groups of two or single predators ($P < 0.05$, Tukey's HSD).

Hunting time

Both the group size of *A. spinidens* and the size of prey instars significantly influenced the duration of hunting time from “touch” to “prey paralysis” ($P < 0.01$, two-way ANOVA; Fig. 2). When hunting sixth instar larvae of *S. litura*, hunting time was significantly longer than when hunting upon third and fourth instar larvae ($P < 0.05$, Tukey's HSD). Hunting time was significantly longer for single *A. spinidens* compared to groups of four when preying upon sixth instar larvae ($P < 0.05$, Tukey's HSD).

Predation success

Predation success was significantly higher for groups of four and groups of two when preying upon third and fourth instar larvae, and for single individuals preying upon third instar larvae than for single individuals preying upon sixth instar larvae ($P < 0.05$, Fisher's exact probability test; Fig. 3).

Table 1 Influence of prey instar and group size on the number of attacks by each *Andrallus spinidens* nymph

Factor	SS	df	F value	P value
Prey instar	1508.6	2	113.99	<0.001
Group size	116.9	2	8.83	<0.001
Prey instar \times Group size	152.4	4	5.76	<0.001

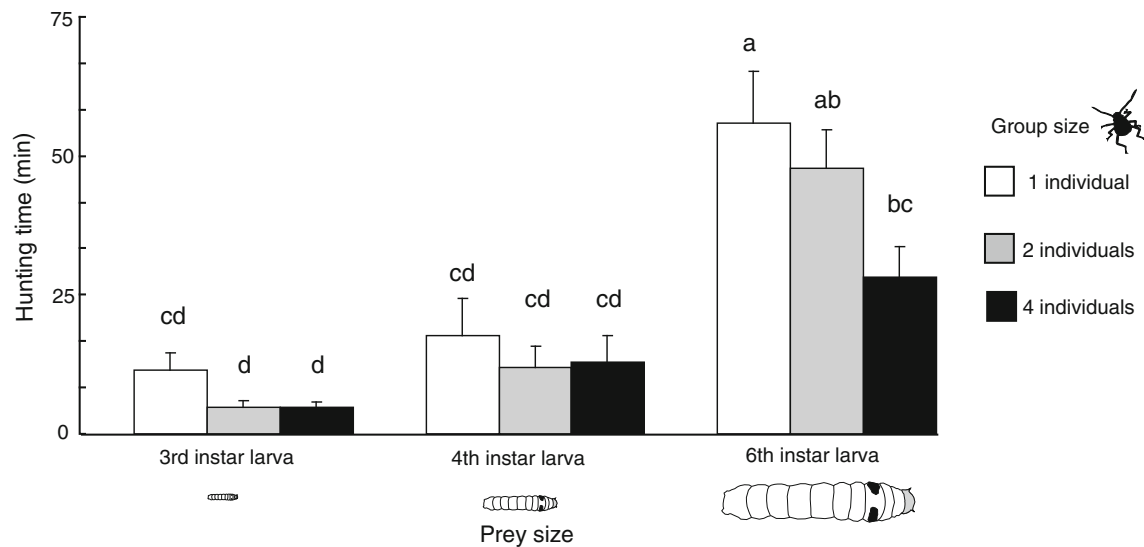


Fig. 2 Hunting time of *Andrallus spinidens* nymphs preying on *Spodoptera litura* larvae. Different letters indicate statistically significant differences according to Tukey's HSD test ($P < 0.05$)

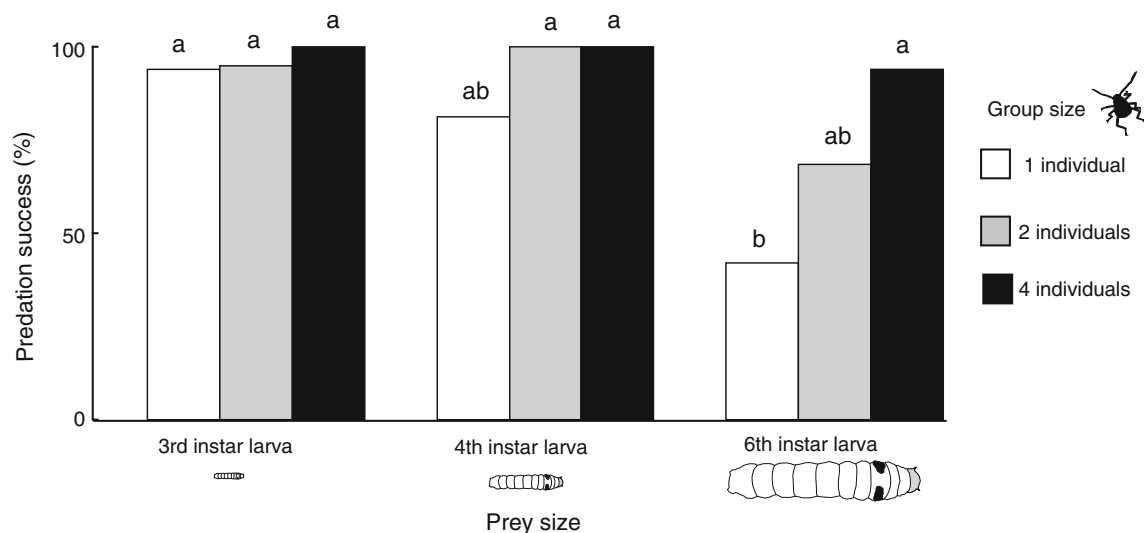


Fig. 3 Predation success rate of *Andrallus spinidens* nymphs on *Spodoptera litura* larvae. Different letters indicate statistically significant differences according to Fisher's exact probability test with sequential Bonferroni correction ($P < 0.05$)

Weight gain

Mean weight gain differed significantly among group sizes (Fig. 4). In tests with third instar *S. litura* larvae, weight gain differed among all three group sizes with smaller groups having greater individual weight gain (Kruskal–Wallis test, $P < 0.05$). In tests with fourth instar larvae, single individuals showed greater weight gain than individuals in groups of four (Kruskal–Wallis test, $P < 0.05$). When hunting sixth instar larvae, individual predator's weight gain was greater when hunting in groups of four than in groups of two, and weight gain for

solitary individuals was intermediate (Kruskal–Wallis test, $P < 0.05$).

Discussion

We found that the costs and benefits of group predation by *A. spinidens* nymphs varied with prey size. In tests with small prey, no significant differences were detected in the number of attacks by each nymph, hunting time, or predation success due to the group size of *A. spinidens*. Under these conditions, mean weight gain was significantly higher

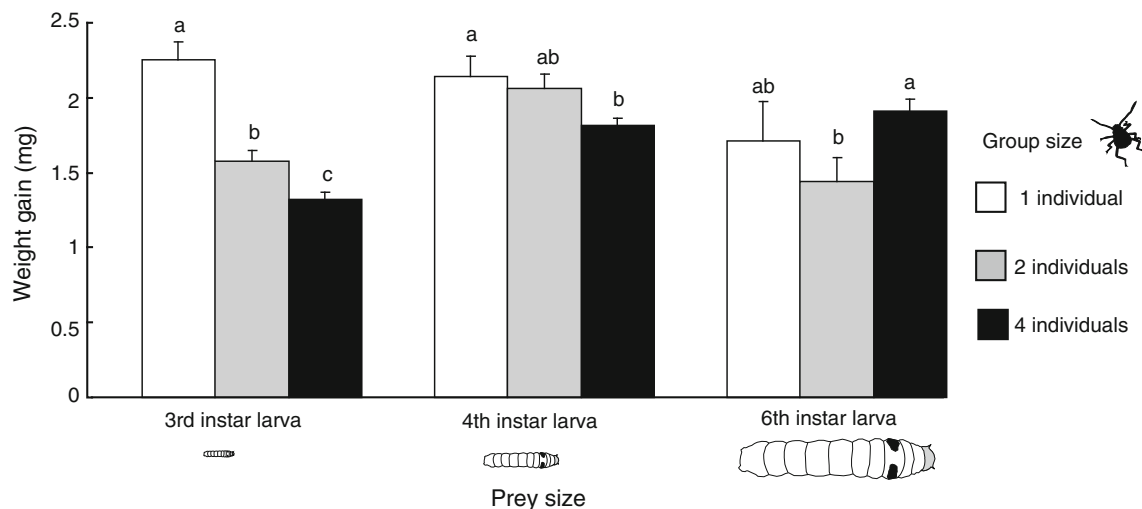


Fig. 4 Weight gain of *Andrellus spinidens* nymphs preying on *Spodoptera litura* larvae. Different letters indicate statistically significant differences according to a Kruskal–Wallis test with sequential Bonferroni correction ($P < 0.05$)

for single individuals than for grouped individuals. Thus, group predation did not significantly promote foraging efficiency with small prey and increased exploitation competition among group members over food. In contrast, in experiments with sixth instar prey larvae, groups of four individuals captured prey with fewer attacks and shorter hunting times, and achieved higher predation success than single individuals. No significant difference was noted in weight gain between single and grouped individuals. Thus, with large prey, group predation for groups of at least four individuals promoted foraging efficiency, and enough food for four individuals.

Such a difference in costs and benefits with the prey size and group size is consistent with results from other group hunting predators, including carnivorous animals, spiders, and insects (Caraco and Wolf 1975; Inoue 1985; Kim et al. 2005). For example, in the African wild dog *Lycaon pictus*, predation success, prey mass, and the probability of multiple kills increased with the number of adults (Creel and Creel 1995). Predation success and the range of prey species attacked have been shown to increase with group size in lions (Funston et al. 2001) and hyenas (Holekamp et al. 1997). However, data from a range of social predators suggest that hunting success initially increases, then levels off or even declines with group size despite cooperation among hunters (Caraco and Wolf 1975; MacNulty et al. 2012).

This study clearly showed that the costs and benefits of group predation for individual nymphs of *A. spinidens* varied with prey size, and suggested that group predation by *A. spinidens* nymphs is advantageous when hunting large prey. Nakazawa et al. (2013) indicated that capture success of juvenile predators generally declines as the prey

size/predator size ratio increases. These results suggest that group predation is favored by early nymphs because of their smaller size and narrower range of prey than older, larger nymphs. This is supported by field observations that group predation by *A. spinidens* nymphs occurs most frequently in second, and to a lesser degree, third instars, while fourth and fifth instars are mostly solitary hunters (Manley 1982). Some other predaceous pentatomids are also reported to be gregarious in the early nymphal periods (see De Clercq 2000), indicating that foraging efficiency may promote group living in the younger nymphs of these insects as well. Further studies examining the costs and benefits of group predation for older nymphs will contribute to understanding mechanism of gregarious behavior of predaceous pentatomids.

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